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Primary Focus Trees for the Mountain Pine Beetle in the Black Hills

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During the early part of the 1991-92 attack periods of the mountain pine beetle (MPB), ponderosa pine stands in the Black Hills were examined for primary focus trees—the first trees attacked by the beetles. Once found, a number of characteristics were recorded for each primary focus tree. Lightning strikes, MPB pitchouts, *Armillaria* infections, or physical breakage were present on 58% of the primary focus trees in 1991 and on 61% of the primary focus trees in 1992. The various predisposing factors are discussed as to their relative importance and role in host selection.

Keywords: Mountain pine beetle, *Dendroctonus ponderosae*, ponderosa pine, host selection, *Armillaria*, red turpentine beetle, *Dendroctonus valens*

Introduction

In 1931, Person first suggested that pine trees may be predisposed to attacks by the western pine beetle (*Dendroctonus brevicomis* Leconte). Person proposed that certain trees were killed not because they lacked resistance but because of a more or less definite selection by the beetles. Beetles are attracted to a tree because it emits volatile compounds (Person 1931). These volatile compounds are created by the physiological dysfunctioning of the tree caused by drought, physical injury, or other factors (Person 1931). Once the first beetles attack the tree, they produce a secondary attraction which leads to mass attack of that tree and possibly surrounding trees.

Person's hypothesis led later investigators to study what physical and biotic factors might predispose host trees to attack. In some cases, the results indicated what physical and biotic factors were associated with epidemics and not necessarily whether these factors predisposed the first tree to be attacked. However, the implication was that the associated factor had predisposed the tree(s) to attack and, further, the associated factor caused epidemics—implications not always true.

Early investigators frequently associated endemic populations of the mountain pine beetle (MPB) (*Dendroctonus ponderosae* Hopkins) with physically damaged trees, slow-growing trees, or trees affected by biotic agents. Endemic MPB populations successfully attack decadent trees (Craighead 1925, Blackman 1931), trees on the poorest sites (Blackman 1931), injured trees (Blackman 1931), or lightning-struck trees (Craighead 1925). More recently, endemic MPB populations were more frequently infesting mature lodgepole pine (*Pinus contorta* Douglas) infected with *Armillaria mellea* (Vahl. ex. Fr.) Kummer than uninfected lodgepole pine (Tkacz and Schmitz 1986). Similarly, lodgepole pine with Comandra blister rust (*Cronartium comandre* Pk.) were attacked more frequently than trees without Comandra blister rust but the same could not be shown for trees affected by dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) (Rasmussen 1987).

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MPB populations have commonly been found in trees with root diseases (Cobb et al. 1974, Hinds et al. 1984, Lessard et al. 1985). The high incidence of association of MPB and root diseases in the same trees implies that root diseases predispose trees to beetle attack and play an important role in beetle population dynamics (Cobb et al. 1974). Because virulence varies among root diseases, the predisposition role of each disease is not always clear. For example, the role of *Armillaria* may be secondary (Cobb et al. 1974), becoming primary only when some factor such as drought (Cobb et al. 1974) or other diseases (Kuhlavy et al. 1984) stress the tree and thus allow the *Armillaria* to invade the roots. In the Black Hills, the infection pattern clouds the *Armillaria*-MPB relationship because *Armillaria* may invade the roots after trees died (Lundquist 1991), i.e., after successful MPB attack, thereby misleading investigators as to its predisposing role. In addition, fire may wound the major roots and thus provide infection courts for root diseases (Gara et al. 1985). Which factor is primarily responsible for the predisposition is therefore questionable.

Whether predisposition sets up host selection and prompts the MPB to begin its attacks on a specific tree is still debated (Wood 1982). In any event, the first attacks cause that tree to become the focal point for subsequently attacking beetles—the "focus tree" of Geiszler and Gara (1978). As the primary focus tree fills with attacks, subsequently arriving MPB attack adjacent trees so that they also become focus trees (McCambridge 1967, Geiszler and Gara 1978). Although a variety of physical and biotic factors including drought, fire, lightning, diseases, insect defoliation, and other scolytid attacks are thought to predispose and thereby create focus trees, the relative importance of these factors is unknown.

In this study, we examined the physical characteristics of the primary focus tree—the first tree attacked—for spot infestations during the current MPB epidemic affecting ponderosa pine (*Pinus ponderosa* Lawson) in the Black Hills.

Methods

We surveyed 2 areas on the Black Hills National Forest about 10 miles northwest of Custer, SD. Parts of sections 1, 12, and 13, T.45N., R.3E. comprised one area and parts of sections 10 and 15, T.45N., R.3E. comprised the other area. The first area was searched in 1991 and 1992 but the second area was searched only in 1992.

The general area has been exposed to a natural MPB epidemic since the mid 1980s. Tree mortality in Bear Basin, where the current MPB epidemic apparently originated, was readily apparent in 1987. The epidemic expanded in 1988 and 1989 so that groups of 5 to 20 infested trees appeared in the upper Spring Creek and White House Gulch drainages (Schmid et al. 1993). By 1990, larger groups of 25 to 50 infested trees were evident in the landscape outside Bear Basin. Tree mortality in Bear Basin averaged 5.9 trees per acre for 1989, 17.8 for 1990, and 37.6 for 1991 (Pasek and Schaupp 1992).

We searched for primary focus trees from July 29 through August 7, 1991 and from July 30 through August 5, 1992. The two areas were searched rather than Bear Basin because we thought that the availability of trees exhibiting the gamut of host conditions would be greater in areas where previous tree mortality was less extensive and had not largely depleted the stands.

Two general approaches were used: (1) Locate a currently infested group of trees and examine green uninfested trees surrounding the group for new primary focus trees in ever widening circles; or (2) search stands with the personnel spaced 30 to 50 feet apart and walking parallel to each other. The first approach was used primarily in 1991 when three workers searched for the primary focus trees. The second approach was used more in 1992 when 7 workers were available. However, even with this approach we tended to search more throughly in the area surrounding a currently infested group because Knight and Yasinski (1956) found 84% of the new infestations were within 330 feet of previously infested groups.

Once a primary focus tree was found, it was flagged and its location mapped. We did not usually thoroughly examine the tree immediately after locating it because immediate examination detracted from locating additional focus trees. However, we returned to examine the trees and record a number of characteristics within two weeks in 1991 and within three months in 1992.

Besides measuring diameter at breast height (dbh), each primary focus tree was examined for unsuccessful MPB attacks from the previous year (pitchout), other scolytid (primarily *Ips* and red turpentine beetle (*D. valens* Leconte)) attacks, evidence of a lightning strike, physical damage such as broken limbs in the crown or porcupine girdling on the bole, and the presence of *Armillaria*.

Trees with unsuccessful MPB attacks from the previous year were considered pitchouts. The number of unsuccessful attacks on the pitchouts varied from 50 to more than 200 per tree, but most pitchouts had over 100 attacks.

Armillaria was considered present if white mycelial fans or resinosis were evident beneath the bark of the bole at ground level or on the roots. We examined nearly all lateral roots for a distance of at least 3 feet from the base of the tree but did not attempt to unearth lateral roots for their full length or unearth those with a tap root nature.

Basal area per acre was determined for the stand surrounding the primary focus tree using a 10-factor prism and the focus tree as the center point.

Two increment cores were taken at dbh from opposite sides of the tree to determine annual radial growth. Annual radial growth on each core was measured to the nearest 0.001 inch for each of the previous 20 years. Phloem thickness was also measured to the nearest 0.001 inch. A periodic growth ratio (PGR) was calculated by dividing the sum of the radial growth for years 1-5 by the sum of the radial growth for years 6-10 (Mahoney 1978).

Because radial growth at breast height is one way to estimate tree growth but may not always provide the best estimate of tree growth, we also estimated total volume growth for some primary focus trees and unattacked trees of similar size (controls). In 1991, we paired a primary focus tree at each of ten sites with the closest unattacked tree of similar dbh. Both trees at the 10 sites were felled and cross sectional disks were cut at about 5 foot intervals from the entire length of the bole beginning about 1 foot above groundlevel. Disks were thus cut from each tree at about 1 foot, bh, 10 feet, and so forth. Radial growth for each of the last 20 years was measured to the nearest 0.001 inch along 4 different radii on each disk. The 4 radii were usually at 90° angles to each other except when branches or damage had caused the growth rings to deviate from being perpendicular to the radius. The 4 radial measurements for each year were averaged. The distance from the center of the pith to the beginning of the growth ring for year 20 was also measured.

These measurements from all the disks were used in two analyses. First, annual radial growth for years 1-5, 6-10, 11-15, and 16-20 in each disk were summed together. Years 1-5 represent the most recent 5 years of growth or calendar years 1987 to 1991, and similarly for years 6-10, 11-15, and 16-20. The radial growths for each 5-year period at each height were compared between primary focus trees and their respective controls using the Wilcoxon matched-pairs signed-ranks test. Secondly, the annual volume of wood increment was computed for each of the last 20 years using the radial growth measurements from the disks at the different heights. The annual volume increment for the primary focus trees was then compared against the annual volume increment for their respective control trees for each of the past 20 years using the Wilcoxon matched-pairs signed-ranks test. To neutralize the influence of slight differences in diameter and height between focus trees and respective controls, we also computed the percent increase in annual volume increment for each tree and compared the percent increases using the Wilcoxon matched-pairs signed-ranks test.

The importance of fire as a factor in the creation of primary focus trees was addressed only indirectly in this study because recent fires were essentially absent from the study area. However, lightning started a fire in May 1992 that burned about 2 acres in the area searched for focus trees. The trees within the 2 acres were examined for MPB attacks in August 1992.

Two series of growing stock level (GSL) plots had been installed within the area surveyed for focus trees; one series was cut in 1990 and the other series was cut in 1991 (J.M. Schmid, unpublished data). Each series had 4 plots; 3 plots thinned to GSLs 60, 80, and 100 or 116, and one uncut control plot. Data from these plots serve as the basis for our statements on logging and the red turpentine beetle (RTB).

RESULTS AND DISCUSSION

ARMILLARIA

Armillaria was found in 12% of the focus trees in 1991 and in 15% of the focus trees in 1992 (table 1). White mycelial fans were not found in the bases of the 1991 trees but were found in the bases of the 1992 trees. Radial growth for the trees with *Armillaria* was between 0.020 and 0.030 inch/year in the 1991 trees and <0.010 inch/year in the 1992 trees (table 1).

In studies of recent endemic MPB infestations[3], *Armillaria* was associated with 28% of the current MPB-infested trees (Hinds et al. 1984), 75% of the previously MPB-killed trees in the northern Black Hills (Hinds et al. 1984), 79% of the stands in the northern Black Hills with MPB infestations (Lessard et al. 1985), and 68% of the stands in the southern Black Hills with MPB infestations (Lessard et al. 1985). The *Armillaria*-focus tree association of 12% to 15% in this study was about one-half of the 28% incidence of *Armillaria* associated with currently infested trees of Hinds et al. (1984) and one-fifth of their 75% incidence of *Armillaria* associated with previously MPB-killed trees.

The significant association of MPB in trees with *Armillaria* suggests that *Armillaria* is predisposing trees to become focus trees. Hinds et al. (1984) could not make a definitive statement regarding predisposition without further investigation, but their statement "significant association between primary insect attack and single trees with advanced root infection" implies predisposition. Statements in their followup study (Lessard et al. 1985) corroborates their thinking. Considering the difference in the incidence of *Armillaria* associated with currently infested trees (28% from Hinds et al. 1984, <15% from this study) as compared to the incidence associated with previously MPB-killed trees (75%), the incidence of predisposition by *Armillaria* during an epidemic may be <30% rather than >75% as they imply.

The larger question, however, is why the incidence in currently infested trees is so much different from that in previously killed trees? On first thought, the answer may lie in the sampling method. Examining roots for the first 3 feet away from the base of the tree does not provide total examination of most roots, especially the terminal portion of the larger roots. Thus, *Armillaria* infections beyond 3 feet go unrecorded. Whether they exert enough influence to predispose the tree(s) remains to be determined. However, sampling method alone does not explain the difference in the frequencies because Hinds et al. (1984) examined roots of both current and past infested trees in the same manner.

A more plausible hypothesis is that *Armillaria* in the bases of the roots and boles of beetle-attacked trees reflects both colonization before and after MPB attack. *Armillaria* is widely distributed in the Black Hills and is more prevalent in some areas than others (Lundquist 1991). Even though *Armillaria* may aggressively infect ponderosa pine (Wargo and Shaw 1985), its presence may be influenced by stress factors such as fire, logging and the MPB (Lundquist 1991). Moreover, *Armillaria* may invade the roots only after tree death (Lundquist 1991)—in this case after MPB attack. As a consequence, the incidence of *Armillaria* in the roots of previously attacked trees may include trees with extensive *Armillaria* infection at the time of MPB attack as well as trees with nonsignificant or no *Armillaria* infection at the time of MPB attack.

Thus, the nature of the difference in the incidence of the *Armillaria* associated with currently infested trees compared to previously-killed trees might be explained as follows. When *Armillaria* is present in stands without established root disease centers, it infects the roots of a small percentage of the trees within the stand as represented by scattered individual trees, and causes reduced growth on some of the colonized trees. It does not colonize the roots of the majority of the trees but may exist as quiescent lesions on roots of some uncolonized trees as Wargo and Shaw (1985) suggest. The colonized trees, especially those with reduced growth, are predisposed to become primary focus trees (i.e., 1992 trees, table 1). The noncolonized trees are not predisposed and the *Armillaria* extensively infects the roots of these trees only after MPB attack.

Physical Damage

Physical damage (lightning strike, dead top, windbroken crown, scars) was present on 12% of focus trees in 1991 and on 38% of the focus trees in 1992 (table 1). Physically damaged trees in 1991 consisted

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[3] Hinds et al. (1984) and Lessard et al. (1985) indicated the MPB population level to be characteristic of endemic MPB infestations but the number of recently killed and currently infested trees in their plots suggests that they were dealing with the transition from the epidemic to the endemic level.

Table 1.—Characteristics of 1991 and 1992 MPB focus trees. Some increment core information not available (NA) because cores were not taken.

Year/ tree	dbh (inch.)	Phloem thick. (.001")	Radial grw. (.001")	PGR	Basal area (ft^2/acre)	Previous MPB attacks	Physical damage	Armillaria infection
91/1	10.9	108	21	.74	100	PO[1]	No	No
91/2	11.7	76	36	.98	100	No	No	No
91/3	13.2	116	75	1.00	70	No	Lightning	No
91/4	12.4	129	4	1.66	100	No	Lightning	No
91/5	12.0	80	40	.94	170	PO	No	No
91/6	10.9	NA	NA	NA	170	PO	No	No
91/7	13.3	132	63	1.35	110	PO	No	No
91/8	14.0	86	52	.85	110	No	No	No
91/9	8.9	64	15	.96	170	No	No	No
91/10	8.1	72	24	.80	110	No	No	No
91/11	9.6	58	34	.96	170	No	No	No
91/12	13.0	76	18	.69	170	No	No	No
91/13	9.0	82	32	.73	170	No	No	No
91/14	9.9	80	33	.89	130	PO	No	No
91/15	10.9	NA	28	.53	130	PO	No	Yes
91/16	11.2	108	42	.66	130	No	Lightning	No
91/17	11.7	124	45	.82	130	No	No	No
91/18	11.7	103	28	.90	NA	PO	No	No
91/19	9.0	82	27	.67	170	PO	No	No
91/20	8.2	73	24	.76	120	No	No	Yes
91/21	18.5	60	26	.70	180	No	No	No
91/22	8.2	83	17	1.09	150	PO	No	No
91/23	10.3	110	20	.82	150	No	No	Yes
91/24	9.7	116	28	1.03	100	No	No	No
92/1	17.6	NA	44	.95	30	No	Lightning	No
92/2	11.8	130	14	.60	90	No	Resin/scar	No
92/3	6.6	56	14	1.54	120	No	Lightning	No
92/4	14.0	81	34	.50	120	No	No	No
92/5	9.7	NA	19	.64	140	No	No	No
92/6	11.2	NA	43	1.49	80	No	Lightning	No
92/7	9.4	102	26	.78	120	PO	No	No
92/8	5.5	41	7	.77	120	No	No	Yes
92/9	13.1	84	22	.62	160	No	No	No
92/10	17.3	104	18	.75	120	No	No	No
92/11	9.2	58	9	.37	70	No	No	Yes
92/12	13.0	NA	54	2.16	110	No	Dead top	No
92/13	11.7	NA	NA	NA	110	No	Broken fork	No

[1] *PO equals MPB pitchout from previous year.*

entirely of lightning-struck trees. Of the five focus trees with physical damage in 1992, three were hit by lightning, one had one fork broken out of its forked top crown by wind in the two months prior to attack, and one had a dead top that was not of recent origin (table 1).

MPB Pitchouts

MPB pitchouts from the previous year comprised 38% of the focus trees in 1991 and 8% of the focus trees in 1992 (table 1). Each pitchout was on the periphery of an infested group and was created the same year the group was infested. The pitchouts received about the same density of attacks per ft^2 at breast height as successfully-attacked trees but attacks rarely extended above 15 feet. The pitchouts resulted from an insufficient number of attacking MPB.

Pitchouts functioning as primary focus trees exemplifies how infested areas can enlarge in ponderosa pine forests. When a pitchout is created on the edge of an infested group of trees, it may become the focus tree for the beetles emerging the following year from the successfully attacked trees adjacent to the pitchout. If a pitchout is created the next year, it becomes a focus tree for the subsequent year and so forth until the MPB population declines. This scenario benefits MPB populations because dispersal mortality would be minimized as most of the population would be attracted to the focus tree or subsequently attacked trees and would not be lost while searching for a suitable host.

Pitchouts as primary focus trees can also explain why so few pitchouts are found in stands formerly subjected to MPB epidemics. Scarred trees are created in lodgepole pine stands by MPB strip attacks and the incidence of such trees should increase during the life of the epidemic (Stuart et al. 1983). However, if scarred trees (i.e., strip attack) or any other type of unsuccessfully attacked tree creates an attraction for the subsequent MPB generation as did the pitchouts in this study, then they could be successively attacked by the next generation of attacking beetles. Thus, the incidence of pitchouts would decrease with the duration of the epidemic.

PGR, Stand Density, and Tree Diameter

Excluding focus trees with *Armillaria*, physical damage, and evidence of previous MPB attacks, the remaining focus trees appeared healthy externally. The PGR values for the remaining focus trees averaged 0.85 in 1991 and 0.63 in 1992 (table 1). Basal area in the immediate vicinity of the remaining focus trees averaged 141 ft^2 per acre in 1991 and 135 ft^2 per acre in 1992 (table 1). Lodgepole pine stands conducive to MPB epidemics frequently have PGRs <0.9 (Mahoney 1978) while ponderosa pine stands have growing stock levels >120 ft^2 per acre (Schmid and Mata 1992). The PGR and stand density attributes of the remaining focus trees were characteristic of stands commonly infested by the MPB.

The primary focus trees ranged from 8.1 inches to 18.5 inches at breast height in 1991 and from 5.5 inches to 17.6 inches at breast height in 1992 (table 1). Thus, the MPB attacked a wide range of tree sizes and primary focus trees were not exclusively composed of large diameter trees.

Radial and Volume Growth

Although radial growth at approximately 1 foot above ground and at breast height in the focus trees for years 1-5 was slightly greater than radial growth for the comparable two heights in the unattacked trees, the differences were not significant (Wilcoxon test, 2-tailed $p = 0.20$ and 0.61, respectively). For the bole sections above breast height, radial growth of focus trees was insignificantly less than radial growth of unattacked trees in all sections except at 45 feet where radial growth of unattacked trees was significantly greater. Annual volume increment of the focus trees was not significantly different than that of the unattacked trees for each of the last 20 years when tested with either actual volume increment or percent volume increment (Wilcoxon test, all 2-tailed $p > 0.09$). Although results for the growth analyses do not indicate clear differences between focus trees and control trees, it may be that trees with an annual growth rate of <0.035 inches per year plus a PGR of <0.85 indicate conditions creating focus trees.

Fire

No 1992 MPB attacks were found on trees in the 2 acres burned in May 1992 even though scorch height reached 5 feet on some trees. Red turpentine beetle attacks were evident on several fire-scorched trees and a group of 1992 MPB-infested trees were observed just outside the fire line. Because MPB were infesting trees in surrounding stands but did not attack any trees within the burned area, we believe that the fire-scorched trees were not attractive to the MPB and certainly much less attractive than lightning-struck or pitchout trees. Our observation agrees closely with observations by Hopkins (1905).

Endemic MPB populations are thought to be associated with fire-damaged trees (Lessard et al. 1985), but the evidence for MPB attraction to fire-scorched trees is minimal. Fire-scorched trees are not preferred by the MPB in ponderosa pine (Hopkins 1905, Blackman 1931), and MPB attacked <1% of the lodgepole pine damaged by the Yellowstone fires (G.D. Amman 1992, unpublished data). MPB did attack some >15 inch diameter trees on the San Juan N.F. in Colorado where scorch height reached above 10 feet (C.K. Lister 1992, personal communication). However, most of the evidence suggests fire-scorched trees are not especially attractive to MPB during the months immediately following the fire. In the long term, fire is more important as a predisposer for root disease infections which later predispose the trees to MPB attacks (Gara et al. 1985).

Red Turpentine Beetle (RTB)

RTB attacks were evident on some of the focus trees, but we were unable to determine that the RTB attacked before the MPB and thereby predisposed the trees to MPB attack. A survey of RTB attacks on leave trees in thinned and unthinned plots showed RTB attacked up to 15% of the leave trees in the thinned plots and <2% of the trees in the unthinned plots (Schmid and Mata 1991). Although some tree mortality occurred in that study, RTB predisposing the trees to MPB attack was not confirmed. During the two years since that survey was conducted, the RTB-attacked trees have not been attacked by the MPB, which suggests the RTB is an insignificant predisposing factor.

Focus Factors, Host Resistance, and MPB Population Levels

Focus trees are created by various events, but not all natural events and human-caused disturbances in ponderosa pine stands appear as important as generally thought. The primary creators of focus trees are lightning, wind breakage of the crown or bole, *Armillaria* infections, and previous MPB attacks. Lightning, wind breakage, previous MPB attacks (pitchouts), and *Armillaria* infection influence the physiological process(es) causing the apparent release of attractive compounds, probably terpenes. The aggregating attraction created by the action of these predisposing factors is strong enough to override the negating effects on attraction derived from reduced stand density and good growth rate. For example, focus tree 1 in 1992 was essentially open grown (BA = 30) and growing well (table 1). Similarly, focus tree 13 in 1992 had a portion of its crown broken out within two months of MPB emergence and became a focus tree despite the fact it was in a well-spaced stand with a basal area of 116 ft^2/acre.

Trees with radial growth rates of <0.035 inches per year in stands with basal area >120 ft^2 per acre but without other predisposing characteristics appear secondarily important until the role of growth as influenced by stand density is better understood.

In contrast, natural and human-caused disturbances such as fire, skidding damage, and RTB attacks appear relatively unimportant as predisposers. Fire rarely creates focus trees during the months immediately following the fire (Hopkins 1905, our data) but may indirectly create focus trees in subsequent years through secondary pathways such as root infections (see Gara et al. 1985). Similarly, skidding damage and RTB attacks may injure the stems of residual trees and attractive terpenes may emanate from the wounds or the attacks; but these trees are seldom attacked (Schmid et al. 1989, Schmid and Mata 1992, J.M. Schmid, unpublished data). Why MPB select trees damaged by natural events—wind breakage and lightning—but do not attack trees damaged by skidding damage or RTB attacks is unknown. Presumably, the emitted compounds would be identical in composition and quantity. Until we identify precisely what the MPB responds to and what is released from the trees, we cannot say why some factors predispose trees to MPB attack and others, presumably creating the same attraction, do not.

The relative importance of the various factors is confusing because the importance of some factors varies with MPB population level and with time. Pitchouts are rarely created when MPB populations are endemic; consequently, pitchouts are unimportant at the endemic level. *Armillaria* infections appear more important with endemic MPB populations than at the epidemic level. Similarly, scolytid attacks—primarily *Ips pini* Say but not RTB—may be important at the endemic level but are of minimal importance at the epidemic level. Lightning, wind-broken tops or boles, and, perhaps scolytid attacks, may also diminish in importance as the time interval between the injury event and MPB attack increases.

The changing role of the predisposing factors at different MPB population levels has influenced our concept of MPB host selection. MPB host selection behavior is considered to differ between endemic and epidemic population levels because of the condition of the trees the beetles attack (Amman 1978, Berryman 1978, Lessard 1981). Endemic MPB populations attack old mature trees of slow growth or lightning-struck trees (Craighead 1925), trees weakened by mistletoe and lightning (Blackman 1931), trees weakened by other scolytids or porcupines, and trees infected with *Armillaria* (Tkacz and Schmitz 1986). In contrast, epidemic MPB populations attack apparently healthy trees (Blackman 1931), large diameter trees with thick phloem (Amman 1978), and healthy ponderosa pine within a diameter (dbh) range of 7.0 to 13.0 inches (Lessard 1981). Some entomologists thus believe this evidence signals a difference in host selection behavior at the endemic and epidemic levels.

We suggest that the basic host selection process in ponderosa pine stands does not change at different population levels but that the host selection process at the epidemic level, as commonly determined by post-mortem surveys, is masked by the magnitude of the number of MPB-infested trees. The results of this study indicate epidemic MPB populations initially select lightning-struck trees, trees with previous MPB attacks, *Armillaria*-infected trees, or wind-broken trees, i.e., those host conditions commonly associated with endemic populations. Because post-mortem surveys during epidemics rarely determine which tree served as the primary focus tree, the logical conclusion is that MPB attacked healthy trees without evidence of predisposition. This is partly true because the vast majority of the attacked trees in a group were probably not predisposed. However, a predisposed tree probably existed within most groups and once the initial MPB attacks create the primary focus tree, subsequently attacked trees are overwhelmed no matter what their condition if sufficient numbers of MPB are attracted into the influence zone of the primary focus tree.

MPB host selection concepts may be further altered with regard to random versus purposive attack. Host selection by bark beetles is considered either a random process in which beetles land indiscriminately on all trees or a purposive process in which beetles land preferentially on specific host trees (Wood 1982) because of some attraction (Person 1931). MPB host selection is considered a random process by Hynum and Berryman (1980). In contrast, Lessard (1981) believes endemic MPB populations preferentially attack (purposive) weakened trees while epidemic MPB populations randomly attack all trees >7 inches dbh. The focus trees in this study suggest the MPB was purposively selecting trees during this epidemic and, therefore, that such selection is not confined to the endemic situation.

The role of primary focus trees also suggests how endemic MPB populations could become epidemic. Endemic MPB populations maintain themselves in *Armillaria*-infected trees, lightning-struck trees, wind-damaged trees, or trees previously attacked by other scolytids such as *Ips*. They may be found more frequently in *Armillaria*-infected trees and *Ips*-attacked trees because these trees are probably more numerous on a per-acre basis than lightning-struck trees. However, MPB populations in *Armillaria*-infected and *Ips*-attacked trees may be unable to increase because tree growth and phloem thickness is poor. While lightning-struck trees are less common than the other two types of predisposed host, lightning is more discriminate with respect to phloem thickness. Lightning has a tendency to strike trees with crowns above the general canopy level. Such trees are more likely to be dominant, large-diameter trees with thick phloem. When lightning strikes a large-diameter tree in the vicinity of an endemic MPB population residing in either an *Armillaria*-infected or *Ips*-attacked tree, the lightning-struck tree is attacked by MPB subsequently emerging from either of these hosts. Brood production in the lightning-struck tree is enhanced by the thick phloem and an increasing MPB population could be generated if climatic conditions favor increased brood survival.

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